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CHAPTER 2

ENVIRONMENTS, ADAPTATION AND EVOLUTIONARY MEDICINE:

SHOULD WE BE EATING A 'STONE AGE' DIET?

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2.1 Introduction

A central tenet of evolutionary or Darwinian medicine is that many chronic diseases and degenerative conditions evident in modern Western populations have arisen because of a mismatch between ‘Stone Age’ genes and recently-adopted lifestyles [1 – 5]. In a nutshell, genes or traits that may have been selectively advantageous or neutral in the past are argued to be potentially deleterious within the context of industrialisation and modernization. Some suggest that this mismatch can be extended even further back in time, to the widespread adoption of agriculture [5]. It is believed that chronic and degenerative conditions persist at such high levels in many populations because the rate at which selection operates is not sufficient to respond to the current pace of cultural and environmental change [1, 5]. In other words, it is thought by many advocates of evolutionary medicine that our environments are evolving faster than we are.

Environments consist of biotic components such as animals, plants and micro-organisms as well as abiotic factors like temperature and topographic features. They exert numerous and varied selective pressures and because human environments differ, environmentally-induced polymorphisms exist. In humans a good example is the high frequency of the haemoglobin S (sickle cell) allele in areas of Africa with endemic *Plasmodium falciparum* malaria [6]. Another often quoted example is the causal link between intensity of UV radiation and skin pigmentation [7]. An albeit more controversial yet increasingly plausible instance of environmental adaptation is the strong selective pressure apparently exerted by climate on several genes involved in regulating blood pressure [8]. Culture also plays an

important part in determining human environments – it is possible for different populations to co-exist in the same physical area but nonetheless experience different environments and therefore selection pressures because of cultural practices. A classic example is lactase persistence in pastoralist populations [9], which tends to be significantly higher than that seen in their non pastoralist neighbours: the cattle herding Fulani and the agriculturalist Yoruba of Nigeria are a case in point [10].

There is thus no question that there are some clear examples of environmental adaptation in human populations, and many of these must have appeared relatively recently and therefore rapidly, since the origin of modern *Homo sapiens* or even since the adoption of specific cultural practices. It is also evident that certain adaptations may no longer be beneficial outside the context in which they evolved: the loss of heterozygote advantage for the sickle cell gene in non-malarial regions, melanomas in light-skinned people in low latitudes and vitamin D deficiencies in dark-skinned people in high latitudes, and differential interpopulation susceptibilities to hypertension and lactose intolerance are but a few examples. The role of relatively recent environments in shaping human variation is recognised in Darwinian medicine. Nonetheless, it is commonly argued that adaptations that have arisen in our recent evolutionary past and which are dependent on a small number of allelic variants do not reflect the true nature and speed of human adaptation to the environment, particularly for complex conditions, such as degenerative diseases, that involve many genes [5]. In these cases, the ‘Stone Age’ is seen as being the environment of evolutionary adaptedness (EEA).

The ‘Stone Age’, as used in evolutionary medicine, is often loosely defined. It sometimes appears to be synonymous with the Pleistocene (the geological epoch that lasted from c. 1.75 million years ago to c. 11 thousand years ago) and at others the Palaeolithic (a more amorphous era that extends from the first appearance of stone tools c. 2.5 million years ago to around 10,000 years B.P). In fact, the ‘Stone Age’ archaeologically encompasses the Palaeolithic, Mesolithic and Neolithic, and so technically should include the period in which plants were first domesticated. In this chapter, the terms ‘Stone Age’ and ‘Palaeolithic’ as descriptors of time are avoided where possible, and instead used only with reference to the general concept of ‘Stone Age’ or ‘Palaeolithic’ adaptations.

Many discussions of ‘Stone Age’ adaptations use reconstructions of past human behaviour based on observations of modern gatherer-hunter groups that inhabit open and arid tropical or subtropical environments (for example the !Kung of southwestern Africa or aboriginal Australians), an assumption that is critiqued below. ‘Stone Age’ diets inferred from such observations apparently show the importance of a variety of plant foods (including nuts, seeds, fruits, tubers and berries) as well as wild (i.e. non-domesticated) animal products, primarily bushmeat or game [2, 3, 11]. Products like honey, fish and shellfish may have been available but are argued to be minor components of the diet [2]. The significance of domesticated foodstuffs, including milk and cultivated grains, is downplayed [2, 3]. Descriptions of ‘Stone Age’ diets stress high fibre foods that are low in salt and high in essential nutrients, as well as having a large protein component [2, 3, 11]. The energy expended in subsistence activities is also highlighted [2, 3], asserting the need for a balance between intake and expenditure.

The concept of adaptation to such a ‘Stone Age’ diet is undeniably seductive. At first glance, environmental mismatch is a plausible theory that explains why we get fat, suffer from heart disease or develop Type II diabetes. The links between these conditions and modern Western lifestyles are well documented, even if the precise mechanisms are yet to be elucidated fully [12]. But is it really accurate to view their occurrence in terms of a conflict between our ‘Palaeolithic’ bodies and rapidly changing modern environments? In this chapter I will consider and critically evaluate notions of the EEA and ‘Stone Age’ adaptation and their utility in understanding human evolutionary history and current human health, focusing particularly on diet. It is not my intention to set them up as straw men. Instead, I am interested in addressing a number of inter-related questions: What EEA? What ‘Stone Age’? What ‘Palaeolithic’ diet? Which populations? Which members of the population? The variation and variability that is not only inherent to humans but also to many successful primates, probably including several hominin species, goes to the heart of these questions. Those engaged in evolutionary medicine should recognise that just as the modern world is complex, the world in which humans evolved was also heterogeneous and not confined to the Pleistocene. The ideas that I synthesise in this chapter are not new; evolutionary biologists, ecologists, palaeontologists and anthropologists have been using concepts of variability and variation to critique notions of the EEA and ‘Stone Age’ adaptations for the best part of two decades [13-21]. However, prominent advocates of Darwinian medicine repeatedly fall back on explanations for some chronic diseases that rely on a homogeneous reconstruction of ‘Stone Age’ environments [4, 5], despite acknowledging the probability of greater complexity [1-3, 22]. I argue that refocusing

hypotheses away from a one-size-fits-all idea that humans are 'imperfectly' adapted to their environments towards a greater appreciation of human variation and variability would strengthen evolutionary medicine and its applications. To these ends, I conclude the chapter by outlining a more flexible, strategic model of human nutrition and suggesting an alternative to the 'Stone Age' diet.

2.2 The Human EEA And 'Stone Age' Adaptations

The 'environment of evolutionary adaptedness' or EEA is the environment or environments in which the current characteristics of a species evolved [23, 24]. Recently, the concept of the EEA has most commonly been applied to humans, adopted particularly by evolutionary psychologists [e.g. 25], but also used in Darwinian medicine [e.g. 1]. However, the theoretical basis of the EEA has been criticised and its practical utility questioned [14, 17]. Of all the criticisms, those most pertinent to the topics covered in this chapter, and which certainly apply to the way the EEA has been used in Darwinian medicine, are that the concept stresses similarities and universals rather than the variation that is necessary for selection [14] and that the mosaic nature of evolution is often disregarded [17]. In addition the idea does not adequately address the fact that selective pressures still operate, leading to the assumption that all evolution has occurred in the past [14].

Tooby and Cosmides [25, p. 388] assert that the EEA is adaptation-specific and comprises a 'statistical composite of environments'. However, they and many others still depend

largely on the Pleistocene as the human EEA. From a general perspective this may be justifiable, given that many of the anatomical and behavioural features that make us human – big brains, obligate terrestrial bipedalism, and complex language and culture – evolved in the Pleistocene. However, as discussed below, the Pleistocene is far from being a uniform temporal and spatial entity. If it is useful to think of a human EEA in the Pleistocene at all, which chronological subdivisions of the Pleistocene are particularly relevant, and which localities? On a more specific level, the Pleistocene is only one period in time that could be classed within the human EEA, and a significant weakness in the way the concept has been applied within Darwinian medicine is that the evolution which occurred before or after the ‘Stone Age’ is rarely taken into consideration [17]. If the EEA is adaptation-specific, different time periods will encompass the EEAs of particular traits [14, 17], and Foley [14] has argued convincingly that if the concept of the EEA is to be used at all it should be within this context. Thus, to take one example, the emergence of high levels of sociality in human evolutionary history would be linked not to the selective pressures of the Pleistocene, but to the much earlier origin of the catarrhine primates [14].

It is therefore obvious that the data used to reconstruct human EEAs, and by extension Stone Age adaptations, are crucial to their ultimate validity. Even if the specific concept of the EEA is rejected as being theoretically flawed, accurate and detailed evidence for the environmental, ecological and behavioural background to human evolution is essential to the understanding of processes that may have impacted on the biology and health of extant human populations. Such evidence can be direct, taken from studies of the fossil and archaeological records, or it can be analogical. Although methodological developments

such as advanced morphometric techniques, tooth microwear and stable isotope analyses have broadened and deepened the ways in which the adaptations of past humans can be examined, it is still necessary to use analogy, which provides a framework for studying human evolution [26]. A range of animal groups [see for example 27] and human populations have been used as analogues, with modern gatherer-hunters and non-human primates being the most common [26, 28]. Of the non-human primates, chimpanzees and Old World monkeys such as baboons are used most often [26, 28]. Models based on analogy have usefully been divided into two main types – those that are simple or referential and those that are strategic or conceptual [29]. Referential models are common in palaeoanthropology and palaeontology [29], and include direct comparison of one anatomical trait, species or population with another. Conceptual or strategic models, in which the emphasis is on identifying the underlying processes that influence a behaviour or trait in the observable world then extending this to the past [29] are also used but, even now, are less common. A conceptual approach relies on gathering detailed data on the past from a range of sources including the archaeological and fossil records and palaeoenvironmental reconstruction, which then form the basis for strategic inference [29].

Work into ‘Stone Age’ adaptations would benefit enormously from a more extensive application of strategic modelling. An apparently pervasive belief in popular discussions of ‘Stone Age adaptations’ is that the lifestyles and ecologies of some modern gatherer-hunter groups provide a window onto the EEA. A recent UK television programme, for example, sent people to the Kalahari to experience a ‘Stone Age Fat Camp’ in the company of the !Kung. Unfortunately, this simplistic perception is also evident in the scientific literature

[2, 3], with insufficient attention paid to the variation observed in modern populations and the archaeological record, despite recent research [11] that makes more of an attempt to address dietary differences. It is rarely acknowledged that there are numerous types of gatherer-hunter lifestyles or that such populations today show the products of evolution and interactions with other human groups in their ecologies, cultures and behaviours [14, 21, 30].

The subsistence strategies observed in modern gathering and hunting populations have evolved alongside agriculture and other economies, and are far from being relic, ancestral behaviours [31]. On this basis, there is no compelling reason why modern foraging lifeways are better examples of the EEA and its products than pastoralist or agricultural populations using traditional, pre-industrialised subsistence practices. Equally, the diets of gatherer-hunters have not been preserved in aspic since the Mesolithic, with food procurement activities in many areas responding to prevailing ecological or cultural conditions [32, 33]. In addition, relatively recent political and social interventions may have marginalised populations engaged in subsistence economies, with the result that observed 'traditional' lifestyles could well be the product of behavioural and cultural changes that have occurred over the past couple of centuries or even a few decades. This is evident, for example, in the Hill Kharia of northern Bengal, whose fluctuations between agriculture and foraging have in part been determined by external social pressures [33], but is not confined to gatherer-hunter populations, as shown by the effects of Soviet collectivisation on the Evenki herders of Siberia [34]. These factors notwithstanding, a highly selective set of modern foraging groups (primarily those living in the Kalahari or

Australian desert environments) are still generally used as referential models for past populations. A strategic approach, on the other hand, would allow the construction of more complex models, based on underlying ecological principles rather than simple analogy, and facilitate predictions of past adaptations and behaviours in a variety of environments and circumstances.

2.3 Variation And Variability In Human Evolutionary History

The use of the EEA in Darwinian medicine has moved it away from its roots in evolutionary psychology and led to increasingly wide applications. However, since the concept of the EEA and how it is often employed have some serious limitations, it would arguably be better for those interested in the significant and substantial links between evolution, environment, health and disease to approach questions from ecological perspectives. These stress the relationships between the organism and its biotic and abiotic environments, and do not rely on assumptions of a uniform environment for all populations or subpopulations within a species, or indeed for a single population through time. Human environments are inevitably complex, with a significant cultural dimension. It is beyond the scope of this chapter to examine in detail all elements of human environments, so as my major aim is to examine the validity and utility of 'Stone Age' adaptations when thinking about modern human health and disease, I will concentrate on aspects that are frequently and relatively reliably reconstructed from evidence in the geological, ethnographic, fossil and archaeological records. In particular, I will discuss variation and variability in physical environments and habitats from the Pliocene to the Holocene, and

diets and foraging behaviours in living and extinct humans and hominins, including intraspecific and intrapopulation dietary variation. Taken together, these form the basis for consideration of human behaviour and lifestyles from an ecological rather than adaptationist perspective.

2.3.1 Physical Environments And Habitats

Today, humans exploit all the major biomes of the world (freshwater, marine, desert, forest, grassland and tundra), a pattern that was probably established during the Late Pleistocene [35]. The ability of hominins to inhabit or exploit a relatively wide range of environments appears to date from at least the late Pliocene and early Pleistocene [16, 35]. Fossil hominins have been recovered from Plio-Pleistocene deposits in East, southern and central Africa. This extensive geographic distribution alone suggests that early hominins would have experienced different types of environments. The potential variability of hominin environments is supported by palaeoenvironmental data that indicate the availability of a wide range of habitats at many Plio-Pleistocene localities, including woodlands, grasslands and tropical forests [28, 36-41]. African environments altered considerably over time, partly in response to global climatic trends [16, 42] but also due to regional processes, like tectonic activity [43, 44]. A single species, such as *Paranthropus boisei*, with a relatively extensive geographic range and a long tenure in the fossil record would have been required to survive in different habitats and ‘ride out’ numerous environmental fluctuations [35, 45]. At Koobi Fora in East Africa, for example, where *P. boisei* fossils have been recovered from horizons dated to between 2 and 1.4 million years

ago, woodland-dominated habitats in the Upper Burgi Member gave way to more open environments in the succeeding KBS Member and edaphic grassland with much less tree coverage in the more recent Okote Member [37].

Dispersal, although likely to have been determined partially by habitat corridors, would have exposed hominins to novel and varied environments, both within and outside Africa [35]. The 1.8 million year old *Homo* fossils from Dmanisi in Georgia demonstrate that extra-African dispersal occurred early in the Pleistocene [46], if not before [47].

Reconstruction of past global biomes indicates that hominins dispersing out of Africa in the early Pleistocene would have needed to exploit diverse habitats, including grassland and temperate forest, during their expansion into Asia and particularly Europe [48].

Archaeological and geological data from early Pleistocene deposits in China suggest that hominins were subject to significant climate (and thus environmental) variability driven by both regional and global processes [49]. The extreme climatic fluctuations of the Pleistocene would have made a significant impact on hominin environments. Although there was an overall trend to more open, arid environments associated with global climatic cooling during the Pleistocene, this was not a straightforward progression [35]. In Africa, data from fossil lakes indicate that the climate made rapid switches between arid and humid periods during the early to mid Pleistocene [50], a pattern that apparently persisted throughout the Pleistocene [51, 52]. There were also substantial habitat differences in East and southern Africa, the two regions that have yielded most of the African hominin fossil record, with East African apparently sampling a much wider array of open and closed habitats than southern Africa during the Pleistocene [53]. Ice sheet incursion and

contraction periodically altered the extent of the major vegetational biomes in Eurasia [54], and changes to the intensity of the annual monsoon and other frequent climatic events like El Niño would have heavily influenced the distribution of different types of vegetation in Asia [54, 55], with concomitant effects on habitats throughout the Pleistocene.

Throughout much of their evolution, hominins would have been subject to climatic and environmental fluctuation. Some of this variation would have happened at scales that corresponded to glacial cycles, acting over periods measured in tens of thousands of years [56]. However, some climate change was much more rapid, such as the short-lived warming events that occurred within glacials [57, 58]. The transition to these stadial periods might have occurred over periods as short as a few decades [57], within one or two generations of hominins, and would have made a major impact on high latitude environments. Superimposed on these climatic events were annual shifts caused by seasonality, which very probably affected even the earliest hominins [59].

Neanderthals are the classic example of hominins that were able to inhabit high latitude regions during rapid climatic and environmental change. Their body proportions (such as relatively short distal limb lengths and large bi-iliac breadths) appear to have evolved, at least in part, from the influence of cold climates [60-62]. However, it was largely their behaviour that allowed them to respond to variations in climate and environment [58]. Like other organisms faced with environmental variability, hominins had the option to evolve morphologically to new conditions, innovate behaviourally or disperse. Neanderthals probably employed the latter two options, surviving some of the most extreme climatic

fluctuations of the Pleistocene, although ultimately their relatively specialised morphology may have prevented them from reacting effectively to the environmental changes of the very late Pleistocene [58].

Modern humans, on the other hand, with more gracile morphology and highly complex social behaviours were very well suited to tracking the vagaries of the environment and were able to exploit marginal habitats [58]. It is evident that modern humans have responded in many ways to different environments. Morphological evolution is demonstrated by, for instance, differences in skin pigmentation [7] and body proportions [63]. Other biological adaptations include lactase persistence [9, 10] and haemoglobin polymorphisms [6]. Significant cultural and social diversity is also observed, some of which might be mediated or driven by the demands of different environments or the ways in which resources are exploited [64]. An excellent example of the importance of culture to human survival in marginal areas is seen in Arctic populations, in which cultural traditions promote social integrity in regions that require a high level of cooperation, and alterations to technology and material culture help accommodate sometimes rapidly changing environments [65]. Pastoralism is another example of a cultural mechanism that enables habitation and use of marginal environments, as low quality plant food, often not suitable as a dietary staple for humans, is converted into high quality animal food [66]. High latitude gatherer-hunter populations also have a high dependency on meat for this reason [30]. In addition, pastoralists and some gatherer-hunters use movement as a means of living with short term environmental shifts. Seasonal movement is evident in many parts of the world, and there is evidence of a long history of this in some areas. In the Arctic, for

instance, it is indicated by archaeological evidence dating to 4000-5000 years B.P [67] and has also been inferred from the earlier Palaeolithic record [68].

Data from palaeoenvironments and the fossil and archaeological records clearly show that responding to environmental variability is the norm rather than the exception in modern humans and was even evident in the congeneric Neanderthals. The adaptive flexibility of hominins may predate the emergence of our own genus, *Homo*. Indeed, as part of the ‘Variability Selection Hypothesis’ it has been argued that important adaptive features of early hominins evolved in response to variable environments [16]. Such features could plausibly include foraging behaviours and dietary strategies [16]. Although most of the hominin species currently recognized were probably not part of the lineage that led to modern humans, investigating their habitat preferences helps to establish that in human evolutionary history, environmental variation (and therefore probably behavioural and biological variation) was common and has ancient roots. Even with a narrow focus on the candidates most likely to have been part of the modern human lineage, it is clear that their environments varied in time and space. Just after two million years ago, the appearance in the fossil record of *Homo ergaster* / *H. erectus*, the first unequivocal member of the genus *Homo* [69], broadly corresponds to an increase in open environments in Africa [42, 56]. However, the apparently swift dispersal of *Homo* out of Africa into Asia, reaching latitudes as high as 40° N in the Caucasus by 1.8 million years ago [46] and northeast China by 1.3 Ma [49], demonstrates that *H. erectus* grade hominins were not confined to arid savanna grasslands in the tropics. Working on the assumption that these dispersed Eurasian populations did not contribute to the gene pool of modern humans does not significantly

limit the importance of environmental variability and potential for adaptive flexibility in the human lineage - *H. ergaster* and descendents in Africa would have been subject to the climatic cyclicity described above, as well as experiencing marked spatial differences in environments, which may well have included dispersal into and exploitation of tropical forest well before the development of agriculture [70]. It is therefore erroneous to assume that modern gatherer-hunters who live in open, arid environments are automatically the best representatives of 'Stone Age' populations and that African savanna grasslands represent the physical component of the human EEA.

2.3.2 Diets And Foraging Behaviours

The marked differences in environments exploited by modern humans, both today and in the past, and the likelihood that hominins from the Pliocene onwards occupied varied and variable habitats suggest that diets and foraging behaviours were similarly diverse. Indeed, intraspecific dietary flexibility appears to be a hallmark of at least some Plio-Pleistocene hominins [45]. To date, the links between flexibility of diet and habitat variation in early hominins are largely circumstantial. However, several non-human primate species inhabit varied environments and exhibit considerable intraspecific behavioural and ecological variation, which includes dietary flexibility. Stable carbon isotope analysis of rhesus macaque hair suggests clear dietary differences between populations living in different regions, which appear to be related to the seasonal availability (or lack thereof) of favoured foods such as ripe fruit [71]. Baboons show dietary variation [72], linked to ecological differences between sites [73], seasonality [74] and factors, such as age, associated with

individual life stages and preferences [75]. Dietary heterogeneity, in time and space, is also seen in other geographically dispersed Old World primates, including the vervet monkey [76] and the black and white colobus monkey [77]. These observations indicate that dietary variability is the norm rather than the exception in many modern primates, especially those that are widely dispersed or exist in fluctuating environments. Using a strategic approach, this would suggest that environmental variability often results in dietary heterogeneity in primates, an association that could be predicted for early hominins.

In modern gatherer-hunter populations there is a close relationship between diet and environment [30]. Temperature, precipitation and solar radiation are key variables that influence productivity and therefore food availability [30]. Habitat productivity, either measured directly or via rainfall as a proxy, is increasingly being recognised as an important determinant of intraspecific variations in body size – an indicator of dietary quality - in tropical non-human primates [78-80]. In humans, which have a much wider geographic distribution, the relationships between productivity and diet in foraging populations are potentially even more important. At higher latitudes and lower temperatures, productivity tends to be less and the number and range of plant foods included in gatherer-hunter diets decrease [30]. One of the reasons that humans, unlike other primates, are able to inhabit these environments is their ability to procure and consume large quantities of meat and/or fish, exploiting marine/aquatic resources and the specialist herbivores that are adapted to eating low-quality plant food. It has been argued that this was a crucial factor in the dispersals and success of Pleistocene hominins into temperate Eurasia [81] and later into extreme high latitude environments in the northern

hemisphere, which have been inhabited by humans for at least 30,000 years [82]. Polar Inuits, who live in areas with exceptionally low primary productivity (around 45 g/m²/yr), only spend around 10% of their time gathering plant foods directly, depending instead on hunting (40%) and fishing (50%) for subsistence [30]. A similar subsistence pattern is seen in at least forty other gatherer-hunter groups [30]. In fact, the high dependence on gathered plant foods (>80%) reported for the archetypal gatherer-hunters, the !Kung and the G/wi from the Kalahari [30], is exceptional in modern terms. This does not mean that some past gatherer-hunter populations were not equally dependent on plant foods. Rather, the crucial point is that dependence on particular food groups may be driven by the environment, and as environments vary, so will diets.

The archaeological record supports the notion that human diets have varied in time and space. Mesolithic gatherer-hunters exhibited significant dietary heterogeneity, even within a relatively small area like Britain and Ireland [83]. Stable isotope analysis suggests that individuals, grouped by site, had differential dependence on terrestrial and marine resources, with some having mixed diets and others appearing to subsist almost entirely on terrestrial foods [83]. At the well-known British site of Star Carr, over thirty potential plant and animal foodstuffs (birds and mammals) have been identified [83]. Potential dietary variability is also emphasised by the recovery of wild mammal (cattle, deer and boar) bones from Danish shell mounds [84]. Interestingly, fish and seafood, which have a relatively low profile in many reconstructions of 'Stone Age' diets, appear to have been important components of Mesolithic and Neolithic diets at coastal sites in northern Europe, with plentiful evidence for fish consumption at sites in Denmark [84]. At least one Late

Stone Age site, in Lesotho, also has strong evidence for extensive seasonal exploitation of freshwater fish, despite other data suggesting that routine use of river fish in Africa did not become common until around 5000 years ago [85]. This underlines the links between environmental variation, including seasonality, and subsistence patterns and again demonstrates that there was no single or typical dietary strategy in humans during the Pleistocene and early Holocene.

Human dietary variation is not restricted to between-population differences. Significant within population variation in subsistence activity also evident, based on sex, social position, or age. For example, those who hunt, often adult males, may have preferential access to game compared to other members of the population [84], although a simple ‘man the hunter, woman the gatherer’ sexual division of labour is certainly not observed in all populations [30, 86]. Children’s roles in modern gatherer-hunter food procurement are not universally defined. !Kung children do very little foraging, mainly because of the patchy nature of their food resources and the need to travel considerable distances in search of food [87]. They therefore have little control over what they eat, whereas Hadza youngsters are able to forage very near their homes and thus have greater opportunity to determine their food consumption [87]. Children in foraging populations may also choose to procure and eat foods that adults may reject or search for foods in locations normally avoided by adults, as demonstrated by the behaviour of Meriam juveniles in the Torres Strait [88]. It has been argued that perceptions of diet derived from ethnographic research may be skewed because the mainly male ethnographers may not have interacted routinely with women [19], and by extension those dependent on women, like children. This has

implications not only for the accurate reconstruction of diet across a population but also for the ways in which dietary variability and variation are perceived. It is illogical to develop a theory of ‘Stone Age’ adaptation based on the diets of one sex, social class or lifestage, but failure to acknowledge intrapopulation variation leads to such a risk. This again shows the need to consider the importance of human dietary, environmental and behavioural diversity when working within the framework of Darwinian medicine.

2.4 Adaptation And Maladaptation

The brief review of environmental variation and variability as indicated by habitats, diets and intrapopulation differences presented in this chapter only scratches the surface of the diversity evident in modern, past and extinct human populations. Nonetheless, it is clear that reconstructing ‘Stone Age’ adaptations and a typical human EEA is very difficult. The utility of these concepts as they are currently applied in evolutionary medicine is questionable on this basis alone. In addition, much of the work on ‘Stone Age’ adaptations relies on identifying the transition point at which ‘adaptation’ turns into ‘maladaptation’. The boundary between the Mesolithic and the Neolithic is often assumed in theories of ‘Stone Age’ adaptation to represent a switch from a ‘natural’ mode of subsistence to one increasingly dominated by cultivation – the beginnings of the supposed gene-environment mismatch. However, the evidence that the move to agriculture represented a shift from adaptation to ‘maladaptation’ is far from conclusive [17, 19], and transitions between one mode of subsistence to another appear to be, and have been, fluid and dependent on localised conditions.

Multiple lines of archaeological evidence show the probable importance of a range of gathered and hunted foods, a pattern that does not necessarily change abruptly at the boundary between the Mesolithic and Neolithic [84]. When transitions to domestication occurred it is unlikely that there were straightforward replacements of one way of life with another. This general principle is demonstrated very well by some modern gatherer-hunter populations in which subsistence strategies are highly responsive to external social or environmental pressures, switching, for example, from cultivation to foraging and back again [e.g. 33]. Modern populations described as ‘foragers’ may engage in long-term cultivation alongside gathering and/or hunting, as shown by the sago extraction practiced by the Nuauulu [32]. Along the same spectrum, agrarian or pastoral populations may also forage, pastoralists may cultivate, and groups largely dependent on cultivated crops may also keep beasts. Interaction with those engaged in different subsistence economies is also a reality in many regions. In past populations, true demarcation of different subsistence strategies and assessment of major transitions that could cause ‘environmental mismatch’ may thus be very difficult. This indicates that the use of terms such as ‘Stone Age’ diet fail to capture the complexity of human dietary transitions and thus evolution.

The potentially fuzzy boundaries between different modes of subsistence in the past have implications for the way in which health status is interpreted in relation to changes in diet. Since *Man the Hunter* [89] and the introduction of the idea that gatherer-hunters were the ‘original affluent society’ [90], foraging populations have commonly been viewed as having adequate or even ample leisure time and sufficient food to meet their needs. Closely

related to this is the argument that the health of past gatherer-hunters was favourable in comparison with those who had adopted agriculture [cf. 91], one of the fundamental ideas that underlie discussions of ‘Stone Age’ adaptation. This picture of ‘well adapted gatherer-hunters’ and ‘maladapted agriculturalists’ can be critiqued using several different lines of evidence. The first, that subsistence strategies might not fall neatly into one category or another, is discussed above. A second is that observations of modern gatherer-hunters indicate that foraging societies are not necessarily affluent, experiencing food shortage and resultant insults to both physical and evolutionary fitness. The Ache have been reported as being hungry, preferring more food than they are able to procure, and it is possible that fertility and child survivorship would increase if they consumed more [92]. The usual caveats about inferring past behaviours from modern observations apply, but by placing the evidence from the Ache within a general ecological framework, it is plausible to suggest that a similar situation may have been experienced by some past foragers. It has already been argued in this chapter that seasonality and other environmental fluctuations would have made an impact upon many early human populations, and it is likely that resource fluctuation would have caused periods of undernutrition. This might have been exacerbated by lack of food storage, which can act as a buffer against seasonality. It is also possible that, regardless of seasonal shifts, time was a limiting factor on resource procurement in past foragers. Time is a significant constraint in primate behavioural ecology, and even if resources are plentiful, the time budgeted for foraging could only be increased at the expense of other essential activities including resting, travelling and socialising [93].

Another line of critique comes from skeletal data. Some skeletons of gatherer-hunters recovered from the archaeological record show growth perturbations associated with episodic seasonal stress [94]. Such markers appear to be found frequently in individuals from populations, both agrarian and foraging, that live in areas with marked seasonality and which have restricted resource diversity [94]. Thus, it is not always accurate to distinguish the nutritional and health status of groups based on a straightforward assessment of their subsistence economies. Equally, it is a gross oversimplification to assume that ancient gatherer-hunter groups had better overall health status than agriculturalists or pastoralists. Major diseases and health problems often shift as social organization changes. However, such shifts cannot be attributed solely to the adoption of a new mode of subsistence such as agriculture, and emerging health problems are not necessarily induced by diet. For example, the increase of gastrointestinal infections is often attributed to sedentarisation [17] but it is well known by now that sedentary living is not exclusive to agriculturalists, and has been observed in some modern and past gatherer-hunters, with arguably the most famous archaeological example being the Mesolithic Ertebølle people [95]. Thus, although social organization is often linked to mode of subsistence, there are relatively few unique associations between particular types of group structure and methods of food procurement.

There is also no strong evidence that people dependent on food groups excluded from 'Stone Age' diets, such as milk or domesticated grains and starches, automatically have poorer health than gatherer-hunters or suffer disproportionately from dietary intolerances. Many populations have adopted agriculture, and in non-industrialised economies,

including those that are agrarian, chronic diseases of affluence in people following traditional (i.e. non Westernised) diets are rare [20, 96]. ‘Maladaptation’ is therefore not an automatic consequence of a move away from foraging. In some, possibly many, instances gathering and hunting may be a less than optimal way to exploit a particular environment. For example, the Turkana, a well-studied group of modern East African pastoralists, live in an arid environment that is relatively poor in edible and easily-processed plant resources [97]. Their reliance on the meat, blood and particularly milk of domesticated animals (primarily cattle) allows them to exploit an environment that would otherwise be difficult to inhabit [97]. In addition, they have an armoury of cultural and behavioural responses to environmental insults, including regulation of fertility, out-migration, and activity patterns [97]. Although detailed studies of lactase persistence in the Turkana, a biological response to their chosen environment, are yet to be undertaken, it is likely that they are adapted to the consumption of cow, sheep and goat milk into adulthood [98]. Data on the health status of transhumant Turkana populations are limited but despite high rates of infectious diseases and relatively high rates of infant mortality, low rates of malnutrition and other nutritional deficiencies have been observed [97].

These low rates of malnutrition in combination with data from other populations with a history of milk-based pastoralism [9] illustrate that long-term milk consumption is not universally ‘maladaptive’. It is true that from a global perspective lactase persistence into adulthood is the exception rather than the rule. Nonetheless, given that pastoralism might be the most appropriate strategy in unproductive environments, it could have significant nutritional and fitness benefits for those able to digest milk sugar [9]. This environmental

adaptation, dismissed by many commentators on Darwinian nutrition as being a relatively unimportant single allele mutation [5], is a vital element of the ability of some humans to exploit a range of unproductive habitats that would normally be inaccessible to hominoids. The advantages of milk consumption under certain ecological conditions would be hard to identify through a homogeneous ‘Palaeolithic’ view of human nutrition.

Compared to modern diets, starches and carbohydrates, especially from grains, are argued to have been much less important as ‘Stone Age’ energy sources, for which animal protein and fat are seen to be paramount [11]. This is despite strong evidence that starchy foods (including grains), often from a small number of plants, are or were vital dietary components for many modern and ancient human populations, agrarian as well as foraging, in low, mid and high latitude regions [19, 99, 100]. It has also been suggested that starchy underground tubers were vital fallback foods for australopiths in the Pliocene and early Pleistocene [101]. In addition to downplaying the overall importance of many sources of carbohydrate, there is an apparent assumption in ‘Stone Age’ dietary reconstructions that carbohydrates from fruits and vegetables are superior to those from cereal grains [e.g. 2, p. 253], the refined products of which are often seen as being ‘empty’ calories. However, cereal grain refinement of the type evident in Westernised diets is a product of increased industrialisation rather than of grain cultivation *per se*. Far from being deleterious, the consumption of whole grains has been linked to lower incidences of Type 2 diabetes and cardiovascular disease [102, 103].

Another common charge levelled at ‘non-Stone Age’ foods is that they promote food allergies and intolerances, and are thus maladaptive and a further indication of environmental mismatch. Grains, along with dairy products, are often causally implicated by sufferers of the common gut disorder irritable bowel syndrome [104], even though there is no conclusive evidence that these foods promote or exacerbate the condition [105]. In many cultures, regardless of whether or not there is a long history of cereal grain consumption, true intolerance to gluten is relatively uncommon. In the U.K., the prevalence of coeliac disease as diagnosed by serological tests is estimated to be in the order of 1% [106], a pattern that is replicated in many other populations [107]. Interestingly, prevalence is higher in some isolated groups, including the Finnish, the Sardinians and the Saharawis [107, 108].

Although it has been argued that populations with a longer history of grain cultivation and consumption show lower prevalence of coeliac disease [109], current data do not support this theory, with no obvious cline of increasing susceptibility (indicated by disease prevalence and frequency of the candidate HLA-D genes) from the Fertile Crescent region to northern Europe [107]. It is suggested that in the population with the highest reported incidence of coeliac disease, displaced Saharawis in Algeria (in which 5.6% of the children studied tested positive for the disease), high prevalence indicates positive selection for the coeliac disease genotype due to its protective effects against parasites [107, 108].

However, this hypothesis is yet to be adequately tested, and it is also possible (especially given the higher prevalence in other genetic isolates) that stochastic factors, such as founder effect, might also be at work. Thus, although coeliac disease is precipitated by diet

and is undoubtedly debilitating for many sufferers, who may experience reduced fertility, malnutrition and increased risk of certain cancers [106], it is not a particularly common response to the consumption of cultivated grains and its etiology in the context of the development of human subsistence practices requires further clarification. On the basis of current evidence, therefore, general ‘maladaptation’ to cultivated cereal consumption is unlikely, a conclusion reinforced by studies indicating the health benefits of consuming whole grain cereals.

So where does this leave the debate on dietary adaptation versus ‘maladaptation’? In its evolutionary rather than developmental sense, adaptation is genetic, yet few genetic adaptations to diet have been discovered in humans [19]. This indicates that true ‘maladaptations’ to specific diets or ranges of foodstuffs should be rare. In the case of the best-documented example of dietary adaptation, lactase persistence, the ability to digest lactose appears to have tracked milk-based diets, rather than the reverse [9], and (at least until the creeping Westernisation of diets across the globe) adult individuals without this adaptation tended to exist under dietary regimens with no history of milk consumption. It is thus difficult to argue, from an ecological perspective, that the consumption of milk in humans is universally adaptive or ‘maladaptive’ – it is a product of varying environments and thus selection pressures in different populations, leading to polymorphism.

A major implication of the diversity and flexibility evident in human diets is that far from being adapted to a ‘Stone Age’ diet and ‘maladapted’ to Holocene post-agricultural subsistence, modern humans are suited to exploiting and consuming a vast range of

foodstuffs. It has been suggested that the inherent flexibility of human dietary behaviour is a result of our hominoid or even anthropoid origins [19]. This is supported by the evidence reviewed in this chapter, both dietary and environmental. Furthermore, analogy with modern eurytopic primates [71, 75, 76] alongside data from the Old World monkey and early hominin fossil records [110-113] indicate that the broad, plant-based diet (in some cases supplemented by faunal material) characteristic of Old World primates including hominins was established at least by the Pliocene (c. 5 – 2 million years ago), and probably earlier, in the Miocene. Such a diet has been argued to be beneficial to modern humans, albeit with modifications that include increased meat-eating facilitated by technology and decreased dietary bulk [19, 20, 114].

Translated into nutritional advice for humans with Westernised diets high in refined and processed foods, this means eating fewer refined and processed foods and replacing them with fruits and vegetables (and other plants with relatively low digestible energy) as well as opting where possible for grass-fed rather than fatter grain-fed meat [20]. This should be coupled with increased energy expenditure, so that individuals remain in energy balance [20]. This approach to human diet, although based in comparative primatological study (and therefore to an extent drawing on our evolutionary heritage) does not proscribe particular food groups because their widespread adoption occurred in the Holocene rather than the Pleistocene. Instead it encompasses the variability and flexibility that is a hallmark of human subsistence behaviour while identifying the major underlying factors – specifically a limited dependence on highly processed foods coupled with high physical

activity – that appear to prevent chronic diseases of affluence in many populations with ‘traditional’ diets, whether they be foragers, agriculturalists or pastoralists.

2.5 Conclusion: Implications For Medicine

Given the factors outlined in this chapter – environmental variation and consequent dietary flexibility that can be traced back to the earliest hominins and possibly to the radiation of Old World primates, indistinct transitions between different modes of subsistence, and few actual dietary ‘maladaptations’ - it is unlikely that Western diseases of affluence can be explained simply with reference to ‘Stone Age’ adaptations and environmental changes that began with the origins of agriculture. Rather than there being a mismatch between our ‘Palaeolithic’ bodies and modern environments, it is much more likely that diseases of affluence are the result of decoupling intake and expenditure, mechanisation of the modes of production, with consequent industrial processing of food, and living longer. Our bodies are not poorly adapted to cultivated foods *en masse* – in fact, humans have few true genetic adaptations to diet compared to many other animals [19]. Instead, by highly processing food it is made more energy dense, so more calories are consumed before satiety is reached. This leads to weight gain if not offset by activity, and it is also possible that foods with a high glycaemic index (such as refined flours), from which glucose is liberated easily, promote fluctuations in blood sugar levels and therefore an increased risk of insulin resistance [115]. Processing food is not a new phenomenon in humans or even hominins: technologies such as stone tools that were designed to aid food procurement have been around for at least 2.5 million years, and gut proportions in modern humans hint at the

importance of food processing – both mechanical and chemical – prior to ingestion [19]. Many starch staples in traditional diets, such as sago, need extensive processing before they are fit to consume [32]. However, industrial-style processing has led to much food being more extensively ‘pre-digested’ than ever before.

Industrialisation (through both the industrial and the agricultural revolutions) was the driving force of the demographic transition in Europe and other Western nations and led to a decline in mortality and fertility, in addition to massive social change in which food production and supply were concentrated in the hands of a relatively small proportion of the population. Such demographic changes, with attendant alterations to diet, are increasingly being seen in less developed nations, with consequent shifts in disease profiles [96], although the European model of the demographic transition is not exactly replicated in currently developing nations, since chronic diseases of affluence are often coupled with a high prevalence of infectious diseases, leading to a double burden on health. This notwithstanding, alterations to diet caused by industrialisation and urbanisation throughout the world have resulted in a massive rise in obesity, heart disease, type 2 diabetes and other chronic conditions associated with diet. It has been argued that rather than the emergence of agriculture representing the transition in human diet from adaptation to ‘maladaptation’, it is much more likely to be the very recent demographic transition that has caused a widespread shift in disease burdens, including those that are diet-related [17].

Adopting a diet relatively low in highly processed foods plus increasing daily activity may be beneficial to health [20]. Although health advice is notoriously complex and often

contradictory, this message is currently being promoted by some public health agencies. In particular, the Harvard School of Public Health advocates a ‘nutrition pyramid’ with physical activity at its base, followed by whole grain foods and plant oils, then fruits and vegetables. Highly processed foods, animal fats and red meats are at the top of the pyramid [116]. Despite its apparent general popularity, there appears to have been little adoption of the ‘Stone Age’ diet by agencies promoting health and well-being. In fact, some clinicians [117, p. 1420] have argued that exclusion diets, specifically the ‘Stone Age’ diet, can be “highly restrictive, socially disruptive and expensive”. This is not a trivial matter. In industrialised and industrialising nations, socioeconomic status is a powerful determinant of environment, in that it influences exposure to certain pollutants, infrastructure (including education and healthcare) and access to food resources. Thus, promoting diets, like the ‘Stone Age’ diet, that involve avoidance of easily available, cheap foods in favour of those that tend to be harder to find or more expensive, may in fact reinforce chronic disease burdens in certain parts of the community. Health stratification of this type is already evident in the UK: between 1970-72 and 1991-93 there was a marked decline in deaths from heart disease in males from social class I whereas the heart disease death rate in social class V, which was only slightly higher than that in social class I in the early 1970s, remained more or less static into the 1990s [118]. Given these figures, it is likely that social inequality is a much greater risk factor in chronic disease than mismatched genes and environments.

A proximate and sociological perspective on very recent social factors (for example, migrant populations and their health problems) may well be more valuable in the

understanding of chronic diet-related diseases than one that stresses deeper population histories. This is supported by increasing awareness that developmental insults *in utero* caused by poor maternal nutrition can significantly increase the chances of developing chronic diseases in adulthood [119; see also Chapters 4 and 5]. So does this mean that there is no place for human nutritional advice based on evolutionary or comparative data? It is worth stressing that some of the concepts outlined in ‘Stone Age’ diets are beneficial, in particular the emphasis on physical activity. Other suggestions, like reducing sodium intake, also align well with mainstream nutritional advice and evidence-based studies of chronic disease risk. The adoption of these measures, although probably easier for those of higher socioeconomic status, does not necessarily rely on access to specific resources or facilities or require major modifications to normal lifestyles. As already indicated, the main difficulties that emerge when promoting ‘good’ nutrition on the basis of ‘Stone Age’ reconstructions are the emphasis on animal protein, since the (cheap) meat available to most people is much higher in fat than wild game [19], the exclusion of milk (even in populations where lactase persistence is common) and the exclusion of grain, which in its whole form may actually be beneficial.

Appreciating the variation and variability in human diet and its evolution rather than holding fast to ‘Stone Age’ criteria would strengthen understanding about the foods which are best for humans to eat and possibly facilitate mainstream applications of evolutionary medicine in this area. Although the suggestions of Milton [19, 20, 114] about the importance of a plant-based diet low in processed foods draw on evolutionary principles and comparative behavioural ecology, they do not restrict dietary adaptation to a single

point in time and there is no blanket exclusion of food groups on the basis that they are not 'Palaeolithic'. This approach is thus an excellent model for the ways in which evolutionary perspectives can be integrated into achievable public health strategies. Advocating Milton's model rather than the more fashionable and better publicised 'Stone Age' approach would not only improve the theoretical basis of evolutionary perspectives on nutrition but may also be useful in supporting movements calling for social interventions that improve health (such as better urban planning) and uncomplicated, basic nutritional advice [see, for example, 120].

In contrast to a strongly adaptationist perspective that stresses the universal nature of human biology, an ecological perspective on human diets highlights behavioural flexibility and adaptability in varied and varying environments alongside a very small number of rapid genetic adaptations as being crucial to our understanding of human nutrition. Does this in turn mean that the nutritional advice given to individuals should be tailored to their population histories? To an extent, this already occurs with the widespread recognition that not all people have the gene that enables lactose digestion into adulthood. Official U.S. nutritional advice currently plays on the fact that individuals of different body sizes have different energy requirements, and it has been suggested that a next step may be dietary advice based on genotype [121]. This suggestion was very much 'tongue in cheek' but dietary therapeutics are already used not only for those suffering from certain chronic conditions but also for people at risk of developing them (for example, those with a family history of heart disease). Nonetheless, given the inherent flexibility of human diets and the very few genetic adaptations we have to them, as long as people follow the straightforward

and basic rules of keeping highly processed foods to a minimum and staying in energy balance it is difficult to see many general advantages in 'eating right for your genotype', 'Stone Age' or not.

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